A CRUSTOSE SPHACELARIOID NEW TO NORTHEASTERN NORTH AMERICA: BATTERSIA MIRABILIS

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Until recently, the alga *Battersia mirabilis* Reinke ex Batters was known only from the original collections from Berwick-on-Tweed on the southeast coast of Scotland, made nearly a century ago, and from a single collection near Ladehammeren, Norway (Printz, 1926). It is now also known from the Dutch coast (Prud' Homme Van Reine, 1974) and from several localities in the southern Gulf of Maine between Rocky Point and Manomet Point, Massachusetts. Owing to the apparent rarity of the species and to its widely disjunct distribution, the Massachusetts plants of *Battersia* are here described and compared with the published descriptions and several specimens of European origin.

Battersia mirabilis came to our attention after careful collecting using SCUBA diving equipment and detailed laboratory analysis of samples of the numerous fleshy, brown crustose forms which occur in the algal flora of Massachusetts. At first, a curious ralfsioid crust with erect, short stalked, branched or simple, reproductive axes was observed. Upon closer inspection several characteristics readily distinguished it as a little-known component of the *Sphacelariales*, and later, with more material and study, the little sphacelarioid of Batters (1889), *Battersia mirabilis*, was identified.

Battersia mirabilis seems to be uncommon where it has been found, both in Europe and along the Massachusetts coast. Its occurrence is probably more frequent however, since the diminutive size of the crust (usually less than 1–2 cm. diameter) makes it easy to overlook or to confuse with the juvenile stages of several commonly associated brown crusts. Our knowledge of the species' seemingly preferred habitat, its morphology and the color of the living plant may, in time, aid in the recognition of this species as a more common element of the Massachusetts benthic algal flora.

The morphological uniqueness of this sphacelarian has brought *Battersia mirabilis* considerable attention from both Reinke (1891) and Sauvageau (1900). Both studies supplement the original description of the species by Batters (1889) and attempt to clarify the evolutionary position of the species within the *Sphacelariales.* Dried specimens and the alcohol preserved plants from the original collections of Batters (*leg.* January-February 1888 and October 1889) were the only material available to Reinke and later, Sauvageau.

Subsequent references to this species, prior to those of Prud' Homme Van Reine (1974), are those of Fritsch (1945), Newton (1931) and Parke and Dixon (1968); all refer to the original collections of Batters.

Specimen citation. *Battersia mirabilis,* Berwick-on-Tweed, Scotland, October 1889, *E. Batters.* A single large fragment of this collection is present in the Farlow Herbarium, Harvard University. The specimen was given to E. M. Holmes who included it in his Exsiccatae of "Algae Britannicae Rariores," #105, Fasciculus V, London, 1890. The Farlow Herbarium plant is reproductive, with numerous erect branching axes bearing unilocular sporangia, and is morphologically similar to plants of this species collected from the Massachusetts coast. The plant portions shown in Figure II represent various aspects of the specimen collected from the type locality by Batters.

The plant sent to Dr. W. G. Farlow (probably in the late 1890's) consisted of one large (3–4 cm. diameter at its maximum) fragment of a thick, dark-brown crust; branched reproductive axes bearing numerous unilocular sporangia are abundant on the surface of much of this fragment. All of the sporangia that we have seen from this specimen were devoid of spores or of cellular content.

Vegetative plant body. The vegetative portion of *Battersia mirabilis* consists of one to six overlapping and ultimately stratified layers, each of which in all probability consists of a single plant. Prud'Homme Van Reine (1974) describes both discoidal and filamentous germlings arising from zoospores and developing into mature crusts. Crusts are irregular in outline; 3.0–5.0 cm. in diameter; the upper surface uneven, appearing rough owing to the frequency of overlapping crust lobes, the appearance of the reproductive sori, numerous epiphytic algae, and an abundance of fine detrital sediments. The appearance of the crust in the field is clearly ralfsioid. Without optics, vegetative plants of *B. mirabilis* are virtually impossible to distinguish from such species as

Ralfsia verrucosa (Aresch.) J. Agardh, *Sorapion kjellmani* (Wille) Rosenv. and *Symphyocarpus strangulans* Rosenv.

Crust height is 3–15 cells (100–150μm.); the width of the basal cells range from 25–50μm. (35μm.), while the terminal cell of each filament is considerably smaller, 6.0–18μm. (14μm.), (Figure I). In this respect the crust of *Battersia* resembles *Sorapion kjellmani, S. simulans* Kuckuck and *Symphyocarpus strangulans* and differs dramatically from the structure of most other fleshy brown crustose taxa in the North Atlantic.

Plants of *Battersia mirabilis* are easily removed from rock substratum as large fragments. Crust texture is friable rather than of soft consistency as in *Petroderma maculiforme* (Wollny) Kuckuck, *Pseudolithoderma paradoxicum* Sears & Wilce and *Symphyocarpus strangulans*. Both the upper and lower crust surfaces show parallel cell rows and the rows are frequently arranged in small fan-shaped aggregates. With the aid of a dissecting microscope another distinctive vegetative feature is revealed in the larger than usual diameter (for brown crusts) of many surface cells. The diameter of surface cells and their arrangement in parallel rows or into fan-shaped clusters are of diagnostic value in determining the identity of vegetative plants to this genus.

Cytology. All cells of the crusts of *Battersia mirabilis* contain numerous discoidal plastids which do not appear to have pyrenoids as seen with the aid of the light microscope. Plastids are numerous in mature cells, ranging from 3.5–5.0 μm. diameter. Numerous small vesicles that we have interpreted as fucosan vesicles are present in developing unilocular sporangia and in the vegetative cells supporting the sporangia. In preserved material these vesicles aggregate to form a conspicuous dense mass (Figure I). The cell wall adjacent to the substratum is thickened owing to an outer, slightly pigmented layer in contact with the substratum. The material of this outer wall is yellowish to slightly amber in color. It is either an integral part of the cell wall or is secreted by the protoplast of the basal cells, and may function as a cementing substance.

Reproductive structures. With the aid of a dissecting microscope the crust surface may appear locally crowded with numerous, small, emergent filaments that bear reproductive organs (Figure I). Under higher magnification the filaments are seen to terminate

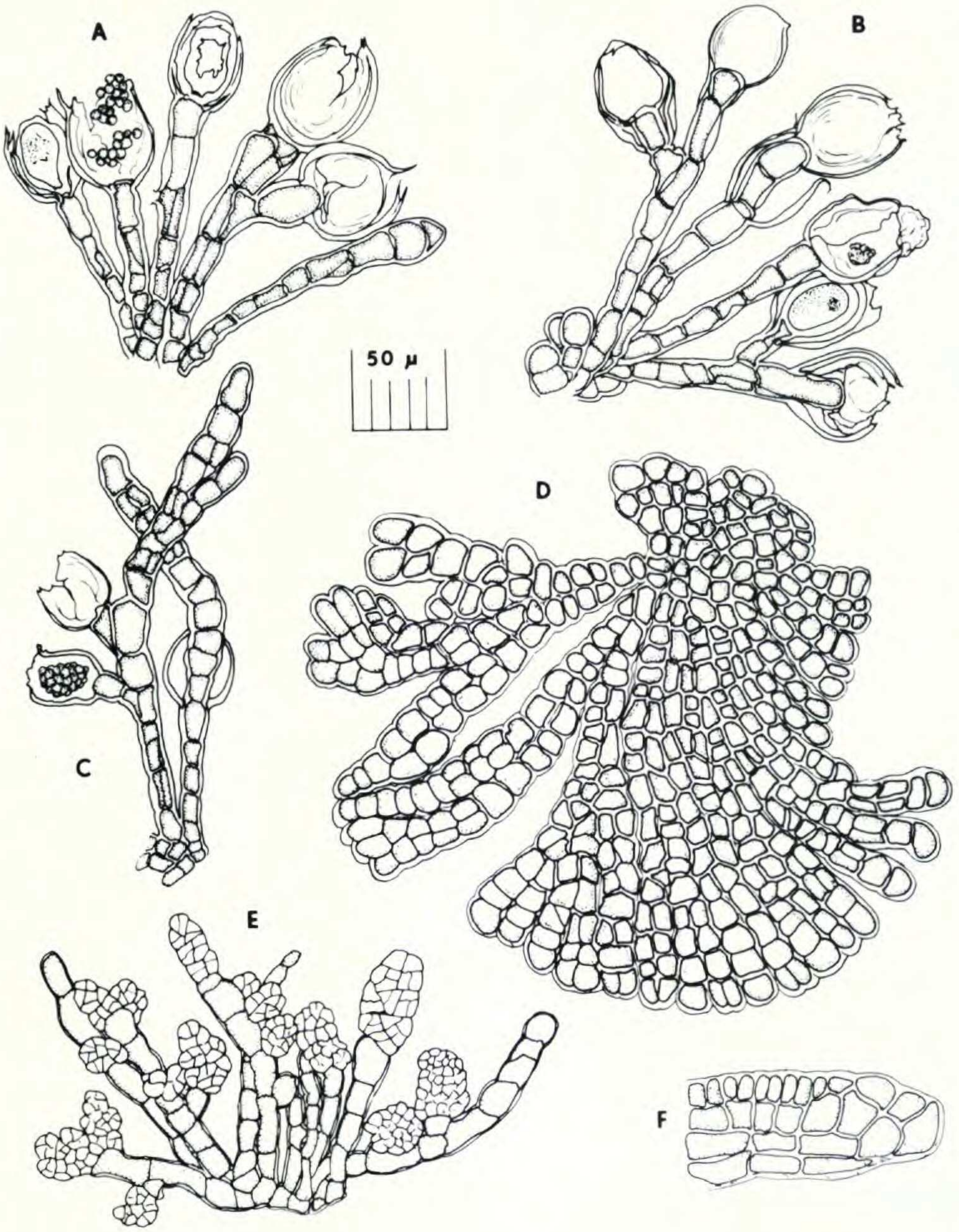

Figure I. Morphological features of plants collected from Manomet Point, Massachusetts: A–C, details of unilocular sporangia and their supporting axes; D, F, different views of the crustose plant; E represents axes bearing plurilocular reproductive organs.

in a vegetative apical cell, a generally globose sporangium, or in a plurilocular reproductive organ; the majority terminate in reproductive organs. The erect filaments of *Battersia,* unlike those of most sphacelarioids, contain cells which do not divide into superior and inferior secondary segments. Some axial cells, however, divide periclinally, resulting in a slightly parenchymatous axis, but these divisions are few. All cells of the erect axes have the potential of initiating lateral development of sessile or short, branch-supported reproductive organs.

Our *Battersia mirabilis* collections of February and May, 1975, include crusts with both unilocular and plurilocular sporangia, the latter newly described for this species. Collections through the summer and autumn, 1975, show only vegetative crusts. Mature sporangia are up to 40 μm. wide, 49 μm. long and are similar to those described by Batters (1889). The width of the cells subtending unilocular sporangia is 13–24 μm. (19 μm.), and the width of the third cell below the supporting cell is from 9–18 μm. (13 μm.). All of the mature reproductive axes that we have seen show a marked basipetal tapering. The plurilocular reproductive organs occur infrequently in our collections. They always occur on separate erect axes from those bearing the unilocular sporangia and may occur singly, terminating an axis, or several short-stalked or sessile sporangia may occur on a single axis. Plurilocular reproductive organs were present in the February collections and present but mostly discharged in the May, 1975, collections.

Propagules have not been recorded for this species and were not present in the Massachusetts collections.

Discussion. Owing to the combination of several characters, *Battersia mirabilis* is clearly sphacelarian. Cytologically it is identical with all of the described species in the *Sphacelariales.* Crust development is thoroughly described by Sauvageau (1900) and compared by him to a similar crust development in plants of *Ralfsia* and *Aglozonia.* Crust structure is filamentous, with lateral growth from marginal initials and growth in height from the divisions of terminal cells. Apical growth and subsequent longitudinal (periclinal) divisions of axial cells, common to most members of this order, occur in *Battersia,* but only in the cells of the upright axes. However, these cells like those of the upright reproductive axes of *Sphacella subtilissima* Reinke (1891), do not form superior and inferior secondary segments common to other members of this order. The appearance of the reproductive axes of *Battersia* is mostly filamentous, but the reproductive organs and their mode of development are similar to the development of these structures in other North Atlantic sphacelarioids. Only the persistent crustose condition of the vegetative plant and the lack of secondary segments in the upright axes set this species apart from other members of the order.

The possibility that *Battersia mirabilis* might be a reduced stage of another sphacelarioid, as suggested earlier by Sauvageau (1900), is not supported by our observations. From the many crusts we have studied, both vegetative and reproductive, there is no indication of a life history association with another member of the *Sphacelariales.*

The single representative of European *Battersia* we have seen is slightly more robust than the largest of our Massachusetts plants. Both crust size and the unilocular sporangia of the European plant average a few microns larger in length and width. The most conspicuous difference in the appearance of the European plant and those from the Massachusetts coast is the high degree of branching in many of the reproductive axes borne on the European plant (Figure II; see also Batters, 1889, *pl. X,* figures 2, 3–3a). Branching in the upright axes of the North American plants is relatively rare and, as yet, we have not seen the "clustered" appearance of sporangia as seen in Figure II, and illustrated previously by Batters (1889) and Reinke (1890). It is likely that the degree of branching is a function of plant age or, if consistently different between the American and European populations, it may have a genetic significance with the result that plants of the two disjunct populations now show morphological divergence.

Battersia mirabilis is yet another northern European species recognized from northeastern North America. The list of such species continues to grow, and the similarities between the two floras are increasingly apparent. A common origin for the two floras appears probable and understandable in the light of current geological concepts and floristic similarities. It is conceivable that several of the northern European species were accidently brought to our coast through human activities. Because these introductions have all occurred relatively recently, they appear to explain the relatively local presence of a handful of species from the total

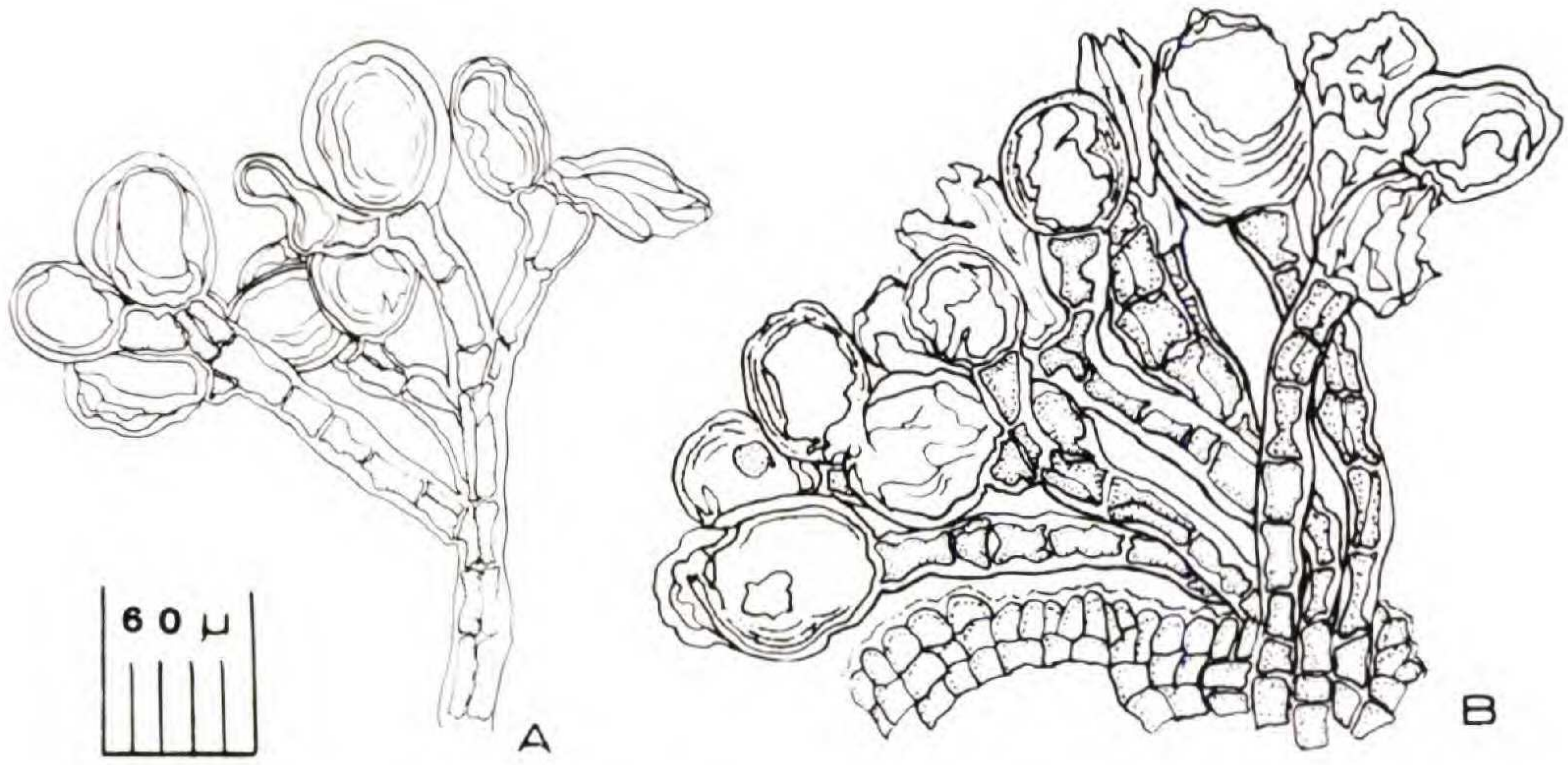

Figure II. Details of the unilocular sporangia and supporting axes of *Battersia mirabilis* collected from the type locality, Berwick-on-Tweed, Scotland, 1889, *leg. E. Batters.*

flora of northeastern North America. It is far more difficult to subscribe to the theory of accidental migration of the greater bulk of the northern European flora to our shores. A single floristic origin, implying considerable antiquity and necessitating extreme genetic conservatism, is the acceptable alternative.

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